

Initial Evidence for the Transport of Teleplanic Larvae of Benthic Invertebrates Across the East Pacific Barrier

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Here is the great immeasurable sea,
in which move creatures beyond number.
Jerusalem Bible, Psalm 104:25.

Abstract. Since the mid-19th century biologists have considered the east tropical Pacific to be a barrier for the dispersal of coastal marine invertebrate species. More recently it has been maintained that this is so because planktonic larvae are unable to cross such a large expanse of ocean. Therefore, it seems extraordinary that no observations have been made to determine whether larvae of invertebrates are actually transported by the major currents of that region. Plankton samples in the present study show that invertebrate larvae do occur within the east tropical Pacific including, but not restricted to, those of gastropods, polychaetes, sipunculans, decapod crustacea, echinoderms, and coelenterates—though as a rule, their occurrence there is significantly less than within the central tropical Pacific.

Data from larval distributions suggest that the east tropical Pacific may act as a substantial impediment to many invertebrate forms, but that it is not a complete barrier to dispersal. Accordingly, the region is best considered a filter. It allows only species with a potential for an exceptionally long larval life to pass *i.e.*, those with teleplanic larvae, while it blocks other forms that are restricted to a shorter time in the plankton owing to an inability to delay metamorphosis or lack of an alternate mode of dispersal. The capacity for dispersal by planktonic larvae differs among the various taxa.

Introduction

There lies within the region bounded to the north and south by the tropics of Cancer and Capricorn, to the west by the Polynesian Islands, and to the east by the Pacific coastline of continental America (*i.e.*, Mexico, Central and northwest South America) and its adjacent islands, the Clipperton, Cocos, Revillagigedo, and Galapagos archipelagos—a vast area of tropical sea devoid of oceanic islands and known to biogeographers as the “east Pacific barrier” (Ekman, 1953) (Fig. 1). Darwin (1860) referred to this wide expanse of open ocean as an “impassable barrier” for the migration of coastal marine species. One hundred years later Thorson (1961) declared that “under average conditions even ‘long distance’ larvae have a much too short pelagic life to survive the critical distance across the eastern Pacific.” Subsequently, other biogeographers have not been so sure. Garth (1965, 1974) found that approximately 50 percent of the brachyuran crabs from the Clipperton Islands in the eastern Pacific were of Indo-Pacific origin and at least 7 Indo-Pacific decapod species found commensal with hermatypic corals were commonly recorded in tropical east Pacific reefs. He attributed this distribution to the dispersal of larvae across the “east Pacific barrier” (Garth, 1966). Briggs (1974) concluded that there “is a one way filter” and that it is possible to speculate that competitive dominant species continue to migrate, as they probably have for a long time, from the Indo-west Pacific toward across the open ocean to America. . . .” Yonson (1978, pp. 253–257) believed from indirect evidence that the one-way influx of Indo-west Pacific species into the eastern tropical Pacific “which may have begun in the Pliocene” was largely the result of dispersal of “long-lived teleplanic larvae,” but supposed that biological and physical factors very likely are also important for the success or failure of

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This paper is for Amélie, helpmate, friend, and colleague in celebration of our one-third century of marriage—October 4, 1988.

emigration to the American continent. On speculating upon the possibility of passive transport of larvae across the east tropical Pacific, Zinsmeister and Emerson (1979) concluded that such dispersal is possible but that the paucity of Indo-Pacific molluscan species is also the consequence of the "vast expanse of open water" and the "lack of suitable habitats with available ecological niches. . . ." Leis (1984) maintained that the hypothesis of larval dispersal across the "east Pacific barrier" must finally hinge upon the demonstration that larvae actually occur within currents of the tropical east Pacific and allowed that "unequivocal crossings of a major portion of the barrier have not been documented." Although there has been much conjecture, the transport of larvae across the "east Pacific barrier" has yet to be demonstrated; indeed it seems extraordinary that over the past century no previous attempt has been made to determine whether any larvae of benthic invertebrates can actually be found in currents of the tropical east Pacific Ocean.

Accordingly, the research described here addresses two fundamental questions. First, is there any evidence that larvae belonging to nearshore species actually occur in the plankton within the region of the "east Pacific barrier"? Second, if so, what invertebrate taxa are represented and is there evidence for differences in the capacity for dispersal among taxa to cross this barrier?

Material and Methods

Plankton samples from the tropical east Pacific were examined from the locations indicated on Figure 1. Samples were taken from collections at the Scripps Institution of Oceanography, including those of the Capricorn Expedition (1952–53), the Eastropac Expedition (1967), and the Domes Expedition (1975–76). Samples were also collected for the present study during: the 73rd scientific cruise of the R.V. KNORR (1979) from the region near Hawaii, the cruise of R.V. THOMAS WASHINGTON on the 3rd leg of the Papatua Expedition (1985) between Mexico and the Samoa Islands, and most recently the Helios Expedition (1987) on the R.V. MELVILLE between San Diego and Tahiti. Most samples were taken obliquely from depths between 150 to 200 meters and the surface, using three-quarter meter diameter and 240 to 360 μm mesh nets. Two hundred and nineteen samples from the tropical eastern Pacific were examined for the larvae of sublittoral benthic species.

Results

Two major currents may transport larvae eastward across the east tropical Pacific Ocean: the Equatorial Countercurrent and Equatorial Undercurrent (Fig. 1; see also Wyrtki, 1965). If transported from west to east, larvae of invertebrates should occur within these currents.

Plankton samples reveal that teleplanic larvae are indeed found within these major equatorial currents. Thus, dispersal within the region of the tropical east Pacific is not only possible but must actually occur. However, the presence of larvae does not prove that the east Pacific barrier is successfully crossed; only faunal data can ultimately show this.

The kinds of larvae encountered encompass a wide spectrum of invertebrate taxa. Samples from within the tropical east Pacific included but were not restricted to (a) veligers of benthic gastropods and bivalves; (b) chaetosphaera, mesotrocha, and other polychaete larval types; (c) pelagosphaera of sipunculans; (d) zoea and megalopa of brachyuran decapoda; (e) plutei, bipinnaria, and brachiolaria of echinoderms; and (f) the *Semper's* cerianthula and planula larvae of coelenterates.

Not all invertebrate groups are equally represented. One example has been selected to illustrate apparent differences that occur in the dispersal capacity among major taxa, at least insofar as this may be reflected by the frequency at which their larvae are encountered in the plankton (Fig. 2).

Gastropod veligers (Fig. 2A) were found in approximately 42% of localities sampled in the eastern tropical Pacific Ocean (as defined in the footnote in Table I) and are represented largely by families already known to have teleplanic larvae (Scheltema, 1986a), e.g., the Architectonicidae (Fig. 3A, B) and Cymatiidae (= Ranellidae). In contrast, polychaete larvae were found at only 28% of all localities sampled (Fig. 2B; 3C–F) and only seldom in the central region of the tropical east Pacific. For instance, only a few teleplanic larvae of the otherwise commonly found polychaete families, Spionidae and Chaetopteridae, are encountered between 120° and 140°W longitude whereas in the central Pacific these families are represented at more than half of the locations sampled (Scheltema, 1986a). Past studies in the Atlantic show that teleplanic larvae in general and the families of gastropods and polychaetes considered here in particular show no discernible seasonal periodicity in their occurrence in the open sea, and that therefore the relative frequency at which larvae are found may be considered as a first approximation a measure of the capacity for long-distance dispersal. If frequency of occurrence is a valid criterion, then there is likely to be a significant difference between gastropods and polychaetes in their capacity for transport across the east tropical Pacific.

The more general question may now be asked: To what extent is the east tropical Pacific likely to be a barrier to dispersal? To gain some insight into this question, one can compare the relative frequency that major taxa occur in the east with that of the central tropical Pacific (Table I). Larvae of decapods, polychaetes, sipunculans, and gastropods occur at significantly lesser frequencies in

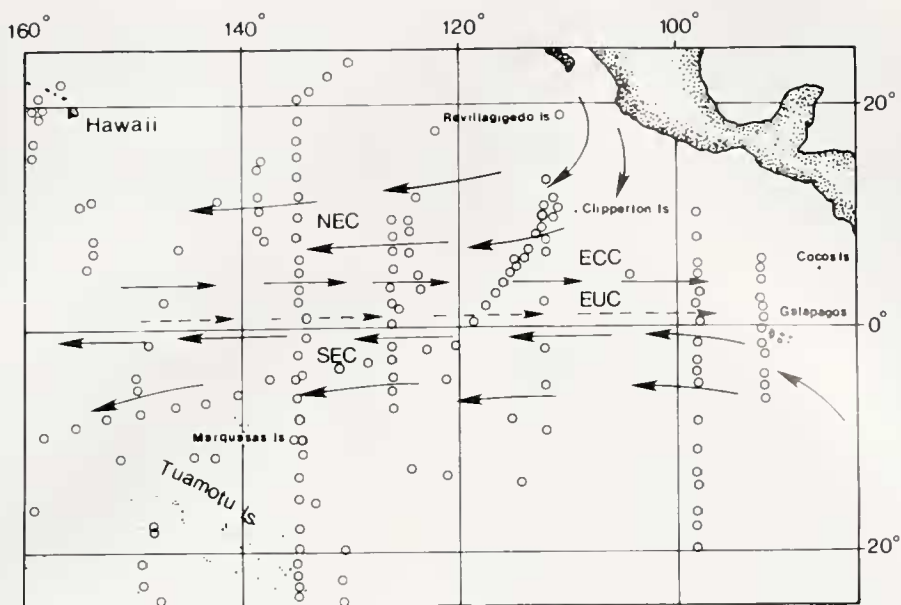


Figure 1. Distribution of sampling locations in relation to generalized surface and near surface currents of the eastern tropical Pacific Ocean. *Open circles* indicate the positions where oblique plankton samples were taken. *Arrows* illustrate generalized patterns of major surface circulation. *Currents from west to east:* Equatorial Undercurrent (EUC) shown by dashed line occurs between 50 and approximately 300 meters depth; the Equatorial Countercurrent (ECC) lies between the surface and approximately 50 meters depth. The Countercurrent is well developed between August and December and absent during February to April. *Currents from east to west:* North Equatorial Current (NEC); South Equatorial Current (SEC). Details of the strength and direction of currents are very much more complex than shown and are subject to seasonal variations (see Wyrtki 1965, 1966 for a detailed discussion).

equal areas of the east than in the central tropical Pacific (compare column 2 and 4, Table I). On the other hand, the *Semper's*, *cerianthula*, and planula larvae of coelenterates evidently are not significantly impeded by the "east Pacific barrier." There are data indicating a greater incidence of echinoderm larvae in the east (47%) than in the central tropical Pacific (16%) (not shown in Table I). This is misleading, since larval skeletons in the older central Pacific samples—some preserved over twenty years—will have deteriorated with time resulting in an underestimate of pluteus abundance (see Scheltema, 1986a; p. 243 for source of central Pacific samples). The table shows that overall the east Pacific may act as a substantial barrier to many forms. The data further suggest that the east Pacific does act as a filter and that it is a significant but incomplete barrier to larval dispersal.

Discussion

Three kinds of evidence can be used to support the hypothesis that larvae may contribute to the spread and maintenance of the Indo-Pacific species across the "east Pacific barrier." Evidence of the actual presence or absence of larvae in the major ocean currents alone may be insufficient because although it admits the possibility,

such information says nothing about the actual success of larval dispersal and its relationship to species ranges. Indirect evidence from the geographical distribution of species is also required to show that the range of an Indo-Pacific form has actually extended into the eastern Pacific. A third kind of evidence indicating that larvae are successfully transported across the east Pacific may come from a comparison of genetic similarity between populations of Indo-Pacific species common to both the central and eastern Pacific. Taken together these three kinds of evidence can allow reasonable inferences to be made regarding larval dispersal of Indo-Pacific species into the eastern Pacific and the likelihood that continuing exchange of larvae in both directions maintains genetic continuity. Separately, each form of evidence has weaknesses and cannot provide a complete answer.

Although the presence of larvae in the plankton provides evidence that dispersal actually happens, their absence cannot prove that it does not occur. The spatial and temporal occurrence of larvae may be such that they go undetected. Larvae that occur at concentrations of less than $1.35 \times 10^{-3} \text{ m}^{-3}$ will not be captured in every twenty-minute tow, yet such concentrations probably are sufficient to act effectively as agents of genetic ex-

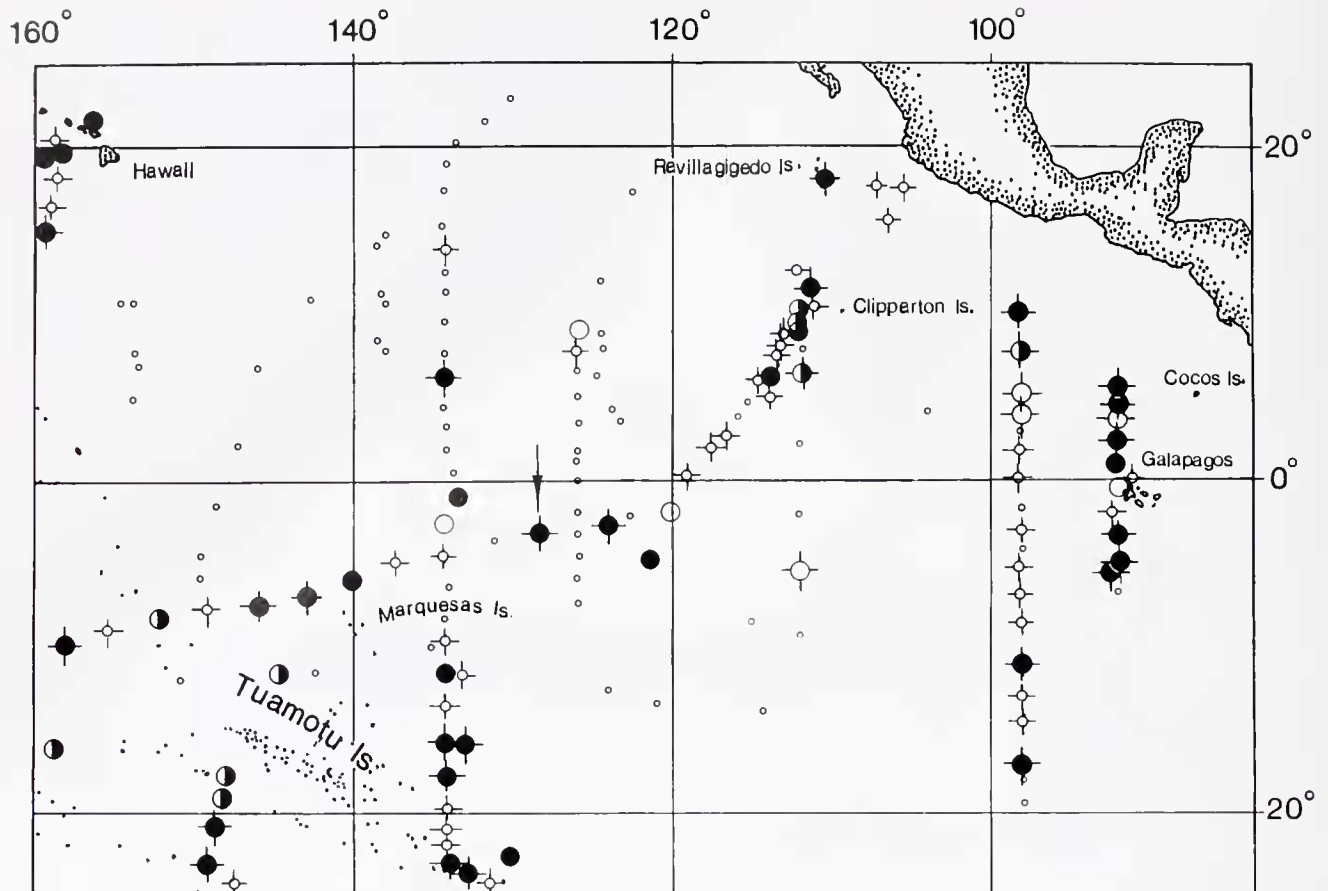


Figure 2A, B. Distribution of teleplanic larvae of coastal shallow-water invertebrates encountered at 219 locations in the open waters of the "east Pacific barrier." A. Locations where veliger larvae of gastropod molluscs were found. *Large filled circles* denote presence of veligers belonging to the family Architectonicidae (see Fig. 3A, B); *large open circles* signify localities where Cymatiidae (= Ranellidae) were recovered; *large half-filled circles* show positions where the larvae of both Architectonicidae and Cymatiidae were encountered; *smaller circles with rays* designate veligers other than those of the two commonmost families of gastropods. *Rays on large circles* indicate that other gastropod veligers were also found. *Minute circles* indicate negative stations where no gastropod veligers were recovered. *Arrow* shows where specimen in Figure 3A and B was collected.

change (Scheltema, 1971; p. 313) and under some circumstances for colonization. Only positive data on the occurrence of larvae are useful; negative data must always remain equivocal. Another familiar source of error may be avoidance of the net as probably occurs among some decapod crustacean larvae.

To ascertain whether larvae of Indo-Pacific species found in the plankton have been effective in colonizing eastern Pacific islands or the American continent, the geographic range of species must be known. In particular it should be demonstrated that the Indo-Pacific species found in the eastern Pacific have planktonic larvae. Return now to the two examples previously used. Among the gastropods Emerson (1982; 1983) reported 49 species of Indo-Pacific prosobranch gastropods in the eastern Pacific. Among these, 38% are known from the mainland

while the remaining 62% are found only on islands (32 species on Clipperton, 3 on Cocos, 9 on the Galapagos, and 1 on Guadalupe). Additional species are attributed by Vermeij (1978) and Shasky (1985). Between 68 and 75 species of Indo-Pacific affinity are now known in the eastern tropical Pacific Ocean. Each year new species are added to the list but the percentage will always remain relatively small (perhaps between 2–3%) compared to the total eastern tropical Pacific gastropod fauna (see Keen, 1971). Most of those species cited by Emerson (1978) are either known to have teleplanic larvae or, if the mode of development is unknown, then belong to families that commonly do. In a study of the polychaetes from Panama, Fauchald (1977) reported 3% (7 spp.) of Indo-Pacific warm-water origin, but his study was restricted to sandy intertidal regions. There were also 28 species re-

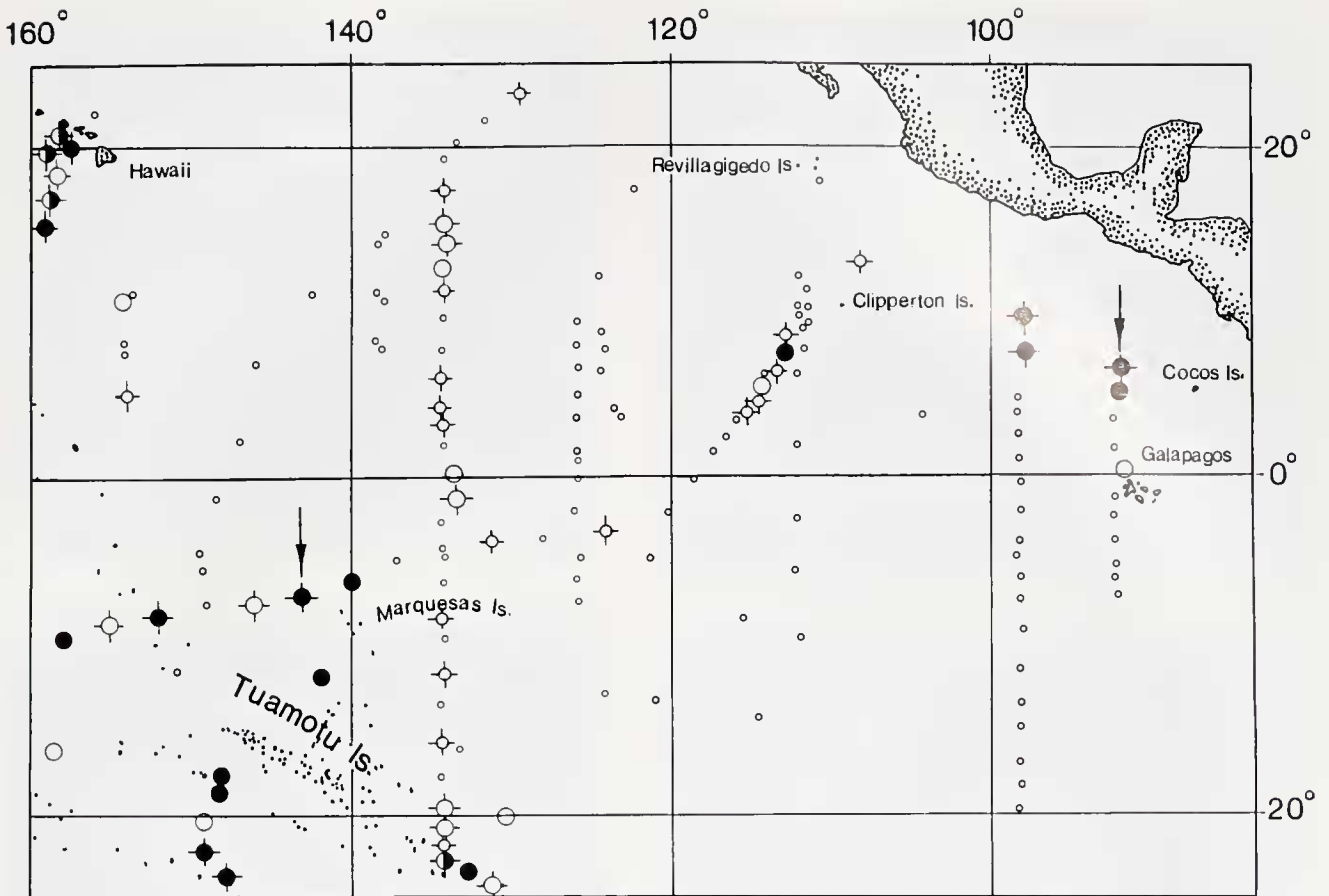


Figure 2. B. Locations where larvae of polychaetes were encountered. *Large filled circles* show where chaetosphera larvae of spionids were located (see Fig. 3C, D, E, F); *large open circles* denote localities where mesotroch larvae of Chaetopteridae were found; *half-filled circles* show positions where both Spionidae and Chaetopteridae were found. *Smaller circles with rays* denote localities where polychaete larvae other than the two most commonly represented families occurred. *Rays on large circles* indicate presence of other polychaete larvae in addition to spionids and chaetopterids. *Minute circles* indicate localities where polychaete larvae were absent in the samples. *Arrows* show points of collection of specimens in Figure 3C, D, E, F.

garded as circumtropical whose wide geographic distribution may be the result of larval dispersal. Since the study was of a restricted habitat, one must consider the data with great reservation. The current knowledge of eastern Pacific polychaetes is probably insufficient to make any broad generalization.

Finally a third kind of evidence, measurement of genetic similarities or differences between allopatric populations, has scarcely been attempted for benthic invertebrate species. Marked genetic similarity between central and eastern tropical Pacific populations of species would suggest sufficient gene flow to maintain the integrity of widely distributed forms. Huber (1985) showed that such gene flow probably occurs between Hawaiian and Panamanian populations of the brachyuran decapod crustacean *Trapezia ferruginea*, since electrophoretic data show no genetic distance between them. To maintain

such similarity, larval or some other mode of dispersal such as rafting (Scheltema, 1986b) would be required, *i.e.*, dispersal is a necessary if not a sufficient requirement for genetic exchange. The potential for such an approach has been further suggested by Rosenblatt and Waples (1986). They showed that populations of 12 species of "trans-Pacific" shore fish (*i.e.*, from Hawaii and the eastern Pacific) are more similar genetically than populations of some of the same species from either side of the Isthmus of Panama.

Although the data on larval dispersal in the east tropical Pacific generally support the hypothesis that dispersal across the "east Pacific barrier" is possible at least for some species, another perplexing problem remains. Is the exchange of larvae completed in only one direction? Most biogeographical studies give evidence for a persistent but small faunal element of Indo-Pacific

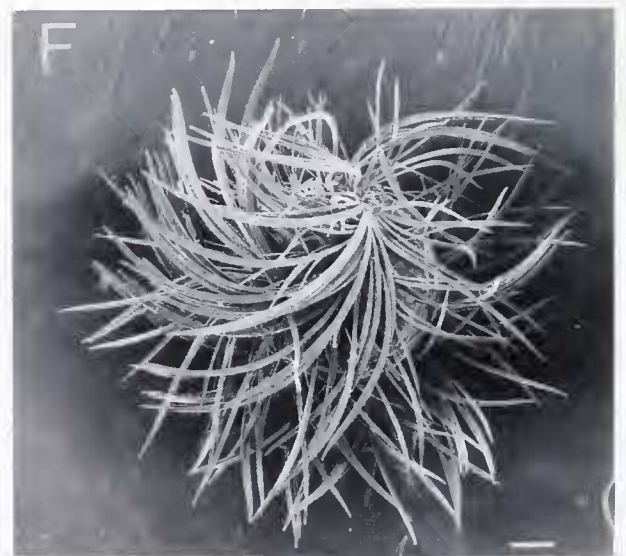
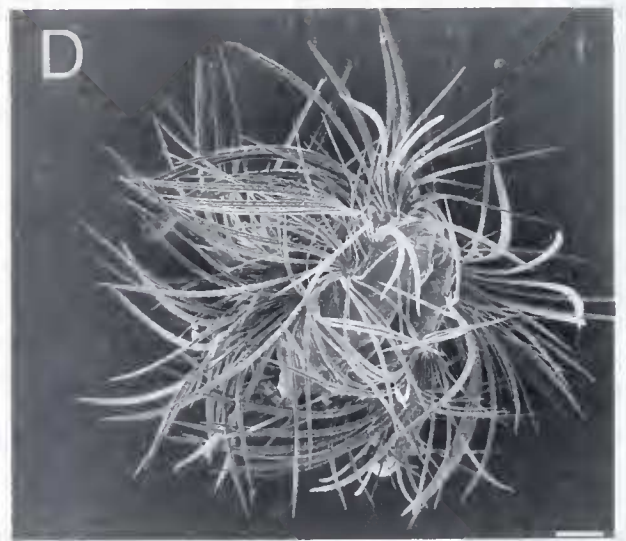
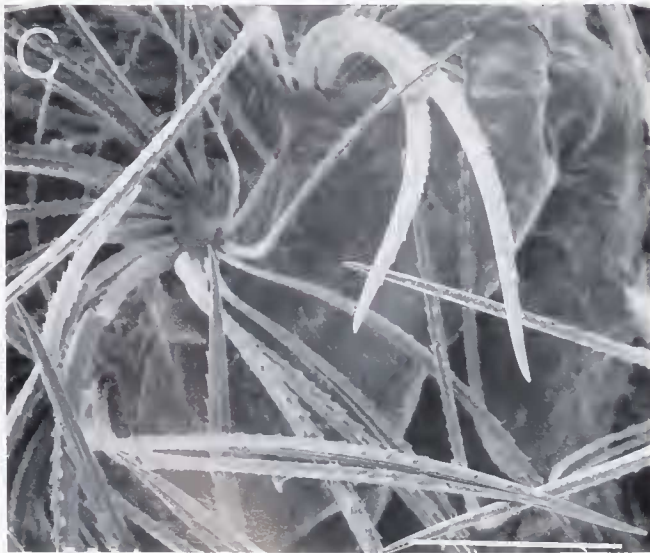


Table I

Differences in the frequency at which the larvae of benthic invertebrates occur in equal areas of the east and central tropical Pacific

	East Pacific Barrier* (total no. sta. = 100)		Central Pacific** (total no. sta. = 129)		P***
	No. sta. (1)	% sta. (2)	No. sta. (3)	% sta. (4)	
Decapoda (zoea, megalopa)	9	9	91	71	0.001
Polychaeta (chaetosphaera, mesotrocha, mitraria, etc.)	28	28	77	60	0.001
Sipuncula (pelagosphaera)	33	33	100	78	0.001
Gastropoda (veligers)	42	41	91	71	0.001
Coelenterates (Semper's cerianthula planula)	66	66	70	54	n.s.

* Tropical east Pacific barrier = 100°W–140°W; 23.5°N–23.5°S.

** Central tropical Pacific = 160°E–160°W; 23.5°N–23.5°S.

*** Value of *P* for χ^2 test of homogeneity (comparison between values in column 2 and 4).

affinity in the coastal east tropical Pacific but none for a complimentary east Pacific fauna in the central or Indo-Pacific (see Briggs, 1974; Vermeij, 1978). The assertion by Zinsmeister and Emerson (1979) that "the absence of warm westward flowing currents has prevented Panamic species with long pelagic stages from reaching the central Pacific" must be mistaken. At least during part of the year, both the westward flowing North and South Equatorial Currents (Fig. 1) have surface temperatures exceeding 26°C. Moreover, larvae of tropical species are actually found in both of these major currents. Consequently, these larvae must be dispersed from east to west (Fig. 2). Temperatures from the surface to the first 50 meters of the North and South Equatorial Currents are well within the range tolerated by tropical teleplanic larvae. The misconception of Zinsmeister and Emerson (1979) may arise from the erroneous notion that the westward flowing North and South Equatorial Currents originate entirely from the California and Peru Currents, respectively. However, Wyrki (1966, p. 62, Fig. 10) notes that between the months of August and December, when it is well developed, the warm countercurrent may, upon approaching the South American continent, con-

tribute up to 37% of the total water mass of the North Equatorial Current. The combined contributions of the countercurrent and undercurrent may somewhat exceed half of the total water mass transported by the North Equatorial Current. Likewise, the countercurrent and undercurrent contribute to the South Equatorial Current during this time of year. Wyrki (1965, p. 274) further concludes that between August and December "the water of the Costa Rica Coastal Current passes directly into the North Equatorial Current." This current, it is supposed, will provide a possible conduit for larvae from the coast of Central America to the North Equatorial Current. However between February and April the countercurrent disappears entirely. Thus, it is obvious that the current system in the easternmost Pacific has marked temporal and spatial variability making predictions about the transport of invertebrate larvae very difficult. The phenomenon of El Niño can add still further variability such as changes in speed and direction of surface currents as well as increase in the surface temperature. Such large fluctuations may provide further opportunities for dispersal of invertebrate larvae which may be unavailable during average conditions.

Figure 3. Representative larvae from the "east Pacific barrier." A. Teleplanic veliger larva of an architectonicid species ($\times 85$) recovered at 3°36.7'S, 128°00.3'W, shown by arrow in Figure 2A. B. Details of same specimen rotated 90° counterclockwise showing umbilical teeth, callus at end of circumapertural varix where it ends on inner lip and fine thread extending around edge of final whorl ($\times 300$). Other larvae of gastropods encountered in the east Pacific barrier include but are not limited to Bursidae, Neritimorpha, Coralliophilidae, Thaiididae, and Cypraedidae. C. Enlargement of the setae ($\times 300$) of the chaetosphaera specimen shown in Figure D. D. Chaetosphaera larva ($\times 100$) belonging to a species of spionid chaetosphaera in the position assumed when disturbed or preserved—recovered from sample taken west of the Marquesas at 7°06.9'S, 142°59.9'W shown by arrow. E. Enlargement of the setae ($\times 300$) of the chaetosphaera specimen shown in Figure F at right. F. Chaetosphaera larva ($\times 65$), possibly the same species as in C and D above, recovered from a sample taken in the east tropical Pacific at 6°04'N, 91°57'W shown by arrow. The larvae appear most closely to resemble type VI described by Bhaud (1986) from New Caledonia. Scales at lower right denote 100 μ m.

One possible hypothesis for the lack of successful dispersal of Panamic species across the east tropical Pacific is the absence of an extensive coastline that westward drifting colonizers may encounter. Only scattered islands provide the possibility for larval settlement. Nonetheless, east Pacific islands for which this argument might also apply apparently are colonized by eastwardly dispersing larvae. There are, of course, other determinates for successful immigration in either direction, for example the access to habitats in which colonizing species can survive and reproduce.

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